AN EXPERIMENTAL STUDY OF THE ATTRACTIVENESS OF ARTIFICIAL PERCH TERRITORIES TO MALE TARANTULA-HAWK WASPS, *HEMIPEPSIS USTULATA* (HYMENOPTERA: POMPILIDAE)*

By William Matthes-Sears and John Alcock
Department of Zoology, Arizona State University,
Tempe, AZ 85287

Introduction

Males of the tarantula-hawk wasp *Hemipepsis ustulata* (Dahlbom) defend perch sites on the highest points of prominent hills and ridges in central Arizona (Alcock 1979, 1981, 1983). A territorial male permits no other male to alight in his plant, be it a palo verde (*Cercidium microphyllum*), jojoba bush (*Simmondsia chinensis*), creosote bush (*Larrea tridentata*), saguaro cactus (*Carnegia gigantea*), or cholla cactus (*Opuntia* spp.). Receptive females sometimes visit a territory site; mating occurs when the resident male captures the female in flight and the pair descends to the ground for a brief copulation. Because defended plants contain no food or oviposition resource for females nor any nests from which virgin females may emerge, males of *H. ustulata* appear to practice lek territoriality (Alcock 1981); they defend areas whose only value to females is the presence of a mating partner.

A striking feature of male behavior is the consistency with which individuals of different generations select certain perch trees from year to year. In one study site many dozens of palo verdes grow on the ridge and yet, every year over five flight seasons the same two trees have been most frequently occupied by territorial wasps (Alcock 1984). A few other trees are almost as popular while some are usually claimed for only a few days of the 2–3 month flight season. The wasps completely ignore the many other trees on the ridge.

We have analyzed the properties of natural territories in order to determine why some trees are so much more likely to be defended than others (Alcock 1984). Males only defend palo verdes growing

*Manuscript received by the editor April 18, 1985

on or very near the backbone of the ridge, not those growing on the slopes. Moreover, the frequency with which males claim a tree is primarily a function of (1) its altitude on the ridge backbone, with trees closer to the peak favored over trees farther down the ridge, and (2) the width of the tree, with large bulky trees preferred over smaller ones.

These results suggest that visual conspicuousness is an important attribute of a preferred territorial perch site for male wasps. They appear to be drawn to large targets clearly outlined against the sky rather than small trees or shrubs whose forms are obscured by a hillside. In order to test this hypothesis we designed experiments in which male tarantula hawks were offered two artificial landmarks in sequence. This gave the wasps a chance to choose between perch sites that differed in their height, size, or contrast. If visual conspicuousness is a key property of a perch site, then male tarantula hawks should inspect and perch on taller, larger, darker targets more often than lower, smaller, and paler landmarks. Our report discusses the response of male wasps in these choice experiments.

Materials and Methods

The experiments were carried out near Usery State Park, Mesa AZ (see Alcock 1979 for a description of the study site) and at South Mountain Park, Phoenix AZ from late March to mid-May 1981 and 1982. Both areas have vegetation typical of the Sonoran Desert of central Arizona.

The experimental landmarks consisted of a pole composed of aluminum tubing supported by a base of metal slats and tubes; the entire structure was painted flat black mottled with tan (Fig. 1). At the top of the pole targets of various sorts were mounted upon which male wasps might perch. Totally artificial perch materials were used to eliminate any effects of familiarity with perch substrates on male choices. The height of the pole could be adjusted by adding or subtracting units of tubing. Each experimental trial consisted of two trials with first one artificial landmark offered to a male after which the landmark was altered and presented again for the same period (either 12 or 15 min, depending on the experiment). The experimental apparatus was erected between 2.5 and 3.0 m from a natural perch site occupied by a territorial male. This wasp

and others patrolling the ridge could investigate or land upon the landmark during the two trials after which the apparatus was moved to a new site. We recorded each "approach" and the total perching time at the various artificial landmarks. An "approach" was scored when a male tarantula hawk flew directly toward the target on the pole and came within 1 m of it. Thus, if a male in a palo verde left his perch and flew close to the perch target, then circled back around his tree and returned to the target (after having traveled at least 2.5 m from the artificial landmark) two approaches were recorded. Perching time consisted of the period from first landing on the artificial landmark until the male left and did not return or until the trial was terminated.

In order to test the effect of landmark height on male tarantula hawks, one experimental perch was set to be about as high (± 0.2 m) as the nearby tree, the other extended by the insertion of more aluminum tubing to be 1.25 m (± 0.2 m) higher. The order of presentation of the two types was established randomly. The same perch target was used in any given set of experiments; in one series of 14 paired presentations, the target consisted of four semicircular pieces of green cardboard, mottled black and tan, fastened onto thin strips of aluminum painted flat black. In another 24 trials, the perch material consisted of green plastic ferns, about 0.5 m long, mounted in an aluminum tube that fitted onto the pole (Fig. 1). Ten of the 24 experiments were conducted in 1981 using four ferns as the target in trials that lasted 12 min each; the remaining choice experiments were carried out in 1982 using five ferns as the perch target in trials that lasted 15 min each.

In order to test the effect of perch size, two landmarks the same height but with different perch targets were placed near occupied territories (N = 14 paired trials). Four semicircular pieces of green plastic mesh were fastened at right angles to one another with flat black aluminum strips and mounted on top of the pole. The larger mesh target had pieces 0.5 m × 0.55 m (total area about 0.45 m^2 and total volume about 0.4 m^3); the smaller target was composed of pieces 0.3 m × 0.35 m (total area about 0.2 m^2, with a volume of about 0.09 m^3). Otherwise the shape and structure of the two targets was the same; each was positioned about 1.25 m higher than the nearby natural perch. Again the sequence of presentations of the small and large targets was random, and each trial lasted 15 min during which time approaches and perches were tallied.

Fig. 1. The artificial landmark with plastic ferns attached to the top of the aluminum pole as a target-perching site for males of *H. ustulata*.

The same procedure was followed in testing the effect of perch contrast. Here, mesh targets were also used, with the same dimensions as the larger target employed in the preceding experiment, but one target composed of plastic mesh was painted green while the other wire mesh target was painted flat white.

After each pair of presentations, the artificial landmarks were moved to a different tree so that no one resident male was given more than one opportunity to respond to a particular pair of landmarks.

Means are expressed ± 1 S.D.

Results

The Effect of Height on Landmark Perch Attractiveness

When given a choice between approaching or perching on two targets, one of which was elevated 1.25 m above the other, male wasps clearly preferred the higher target (Table 1). When the perching material was cardboard, the wasps approached the taller landmark significantly more often ($W = 284.5$, $p < 0.0001$; Wilcoxon two-sample test). The same result applied to the two experiments in which plastic ferns were employed as a perch target (1981: $W = 147.5$, $p = 0.0022$; 1982: $W = 282.5$, $p = 0.0005$). Although for some reason males refused to take up residence upon the cardboard perch, they regularly did so when the target consisted of artificial ferns, but only on the taller of the two available landmarks ($X^2 = 26.32$, $p < 0.0001$, for the combined 1981 and 1982 results). Of the 17 individuals that claimed artificial landmark perches, 12 were residents in a nearby tree that abandoned their territories to move to the higher but completely unnatural perch sites. The other five

Table 1. The effect of height of artificial perches on the frequency with which male tarantula hawks approached and perched on them during 15-min trials.

Perch Material	Perch Height	Number of Paired Trials	Mean Approaches	Mean Perching Time (min)	Number of Males Perching
Cardboard	High	14	15.1 ± 11.2	0	0
	Low		3.1 ± 4.0	0	0
Plastic Ferns (1981)[a]	High	10	17.9 ± 11.1	5.3 ± 5.6	7
	Low		4.5 ± 4.9	0	0
Plastic Ferns (1982)	High	14	22.2 ± 13.5	5.4 ± 5.2	10
	Low		4.9 ± 5.7	0	0

[a] 1981 trials lasted 12 min each.

males had been patrolling the ridge but stopped in order to perch in and defend the experimental landmarks.

The Effect of Size and Contrast on Perch Attractiveness

The larger of two mesh targets was approached significantly more often than the smaller one ($W = 270.0$, $p < 0.005$, Wilcoxon two-sample test; Table 2). The same was true for the darker of two targets when the choice was purely between a dark and a pale perch target ($W = 298.0$, $p < 0.0001$; Table 3). However, there were no significant differences with respect to perching times because flat vertical perches, whether constructed of cardboard or of plastic mesh proved ineffective in inducing male wasps to land. This was probably not due to an aversion to plastic mesh per se because a perch target constructed of five pieces of plastic mesh cut, curled into cones, and mounted on a pole top in such a way as to resemble the artificial ferns attracted 11 perching males in 16 trials. These flexible cones of plastic moved in the wind, as did the plastic ferns, perhaps providing a more attractive visual stimulus than the immobile flat mesh targets.

Discussion

The results of the experiments show that males of *H. ustulata* are clearly attracted to objects that are tall and large, and that stand out against the sky. Their readiness to investigate tall, large, and dark artificial landmarks, which do not resemble any natural perch substrates, demonstrates that certain visual properties are inherently attractive to the wasps. Indeed a substantial number of males abandoned their perch trees and shrubs in order to take up residence on the aluminum and plastic landmarks, provided only that the artifi-

Table 2. The effect of size of artificial perches on the frequency with which male tarantula hawks approached and perched on them during 15-min trials.

Perch Material	Target Size	Number of Paired Trials	Mean Approaches	Mean Perching Time (min)	Number of Males Perching
Plastic	Large	14	16.2 ± 6.5	0.62 ± 1.4	4
Mesh	Small		8.1 ± 4.5	0.05 ± 0.2	3

Table 3. The effect of visual contrast of artificial perches on the frequency with which male tarantula hawks approached and perched on them during 15-min trials.

Perch Material	Target Contrast	Number of Paired Trials	Mean Approaches	Mean Perching Time (min)	Number of Males Perching
Plastic	Dark	14	10.7 ± 4.6	0.4 ± 1.5	2
Mesh	Pale		1.6 ± 1.7	0	0

cial landmark was taller than the natural one and that flexible, structurally complex perching materials were available at the top of the pole. Perch switches occurred even though the natural sites often had a total volume much greater than the artificial ones. The results then are consistent with the hypothesis that males of *H. ustulata* prefer high, conspicuous points on the skyline as territories.

We can speculate briefly on the adaptive significance of this preference. We begin by dismissing the possibility that males are attracted to certain perches because these are the best sites from which to release pheromonal odor plumes. Although it might appear that males at the highest point would be able to generate the longest odor trail, heated air rising off the hillsides creates thermal updrafts that would carry the pheromonal signal upwards, rendering it ineffectual. Instead, we believe that males select the tallest perches at the highest points in order to inspect their surroundings with a minimum of visual obstruction, and this may help them detect approaching females. If, in addition, receptive females more easily perceive tall, large, and dark objects outlined against the sky and therefore approach these objects more often, then male wasps perched in conspicuous landmarks should gain more opportunities to mate. The competition that occurs among males for preferred perches could then arise as individuals attempt to secure a clear view of incoming females and to advertise their presence to mate-searching females.

To the best of our knowledge this is the first study to identify experimentally what makes a potential territory site attractive to males of a lekking species. Although it is well-established that certain perch-display sites are more attractive than others in such animals as the white-bearded manakin (Lill 1974), the hammer-headed bat (Bradbury 1977), and sage grouse (Wiley 1973), it is

unclear precisely what stimuli are critical in male territorial decisions. There are many lek territorial insects (Thornhill and Alcock 1983), and perhaps these animals offer better opportunities to explore the proximate factors that underlie perch site selection in lek-forming species.

Summary

Males of the tarantula-hawk wasp *Hemipepsis ustulata* defend mating territories centered on individual plants of various species growing on ridges and peaktops in central Arizona. Males will leave their natural territories to investigate plastic and cardboard perch targets placed on top of aluminum poles, preferring higher to lower targets and large targets of high contrast to smaller targets of low contrast presented at the same height. A resident male will abandon his natural territory altogether in order to perch upon an artificial landmark, provided that the landmark is structurally complex and is taller than the shrub or tree that the male has been defending.

Acknowledgments

We thank Uta Matthes-Sears for her help in carting artificial perches through the desert. Jerry Waldvogel provided useful information on odor plumes on hilltops. This work was supported in part by National Science Foundation grant BNS 821 9791.

References

Alcock J.

1979. The behavioural consequences of size variation among males of the territorial wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae). *Behaviour* **71**:322–335.

1981. Lek territoriality in a tarantula hawk wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae). *Behav. Ecol. Sociobiol.* **8**:309–317.

1983. Hilltopping territoriality by males of the great purple hairstreak *Atlides halesus* (Lepidoptera: Lycaenidae): convergent evolution with a pompilid wasp. *Behav. Ecol. Sociobiol.* **13**:57–62.

1984. Convergent evolution in perching and patrolling site preferences of some hilltopping insects of the Sonoran Desert. *Southw. Nat.* **29**: 475–480.

Bradbury, J. W.

1977. Lek mating behavior in the hammer-headed bat. *Z. Tierpsychol.* **45**: 225–255.

Lill, A.

1974. Sexual behavior of the lek-forming white-bearded manakin (*Manacus manacus trinitatis* Hartert). *Z. Tierpsychol.* **36**:1–39.

Thornhill, R. and J. Alcock.

1983. *The Evolution of Insect Mating Systems.* (Cambridge, Mass.: Harvard University Press, ix +547 pp.).

Wiley, R. H.

1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus. Anim. Behav. Monog.* **6**:85–169.